

UPPER PERMIAN INSECTS OF NEW SOUTH WALES. IV.

THE ORDER ODONATA.

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(Plate xii, figs. 1-3; four Text-figures.)

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The association of insects and plants in the freshwater beds of Upper Permian age of Belmont and Warner's Bay, near the shores of Lake Macquarie, is such that it has all along been evident that dragonflies of some kind or other must have been present there. Yet the mode of fossilization appears to have been distinctly against the complete preservation of wings of large size, and most of the specimens found have proved to be exceptionally small for Palaeozoic types. This may be partly accounted for by the admitted coldness of the climate in Upper Permian times in Australia. But dragonflies of considerable size can exist in an Arctic climate, and there has never been any reason to suppose that they did not exist in the Australian Upper Permian, since a number of fine types have been found in the Upper Carboniferous of Europe and Lower Permian of Kansas.

The first discovery of a fragment of a dragonfly wing was made by Mr. T. H. Pincombe in 1931, in a piece of rock from Warner's Bay. It is a small piece of a rather large wing, showing the nodus and portions of the costa, subcosta, radius and radial sector around it, as far as the beginning of the pterostigma. A further discovery of portion of the posterior margin and cellules just above it, of a much crumpled Odonate wing, was also made by Mr. Pincombe in 1931.

The above-mentioned material was considered by me to be too fragmentary for description by itself. The search for a more complete wing has now at last been rewarded, twenty years or so after the original discovery of the Belmont Beds by Mr. John Mitchell, by the finding of a nearly complete forewing by Mr. M. S. Stanley on 2nd April of this year, in a piece of pale grey shale brought by him from Warner's Bay. Mr. Stanley is to be heartily congratulated on this fine discovery, which is commemorated in the naming of the species in his honour in this paper. The other fragmentary remains are also dealt with in this paper.

It seems best to deal with the descriptions of the new families, genera and species first, and then to discuss their affinities. The known Odonate fauna of the New South Wales Upper Permian can now be classified under the following tentative key:

- Nodal fork with long anterior branch (Sc) and the subnodus (Sn) continuing the line of the short lower branch Genus *Polytaxineura*, n.g.
- Nodal fork with both branches short, and the subnodus descending practically at right angles to R_1 Genus *Antitaxineura*, n.g.

Family POLYTAXINEURIDAE, n. fam.

Dragonflies of moderate size, belonging to the Suborder Protanisoptera. Hindwing slightly broader than fore. A coriaceous precostal area present at base of costa. Costal margin serrated. Numerous antenodals of both series present; apparently only one postnodal present. A complete nodus and subnodus present at a point well beyond half-way along costa, with a marked bend or break at the junction of Sc with C. Radius and media (MA) are distinct though contiguous veins from base to arculus; Rs + MA leaves R₁ at arculus in a very gentle slope. Cu₂ and 1A both strongly curved in an upward hump in the region of the arculus. Discoidal cell of forewing open basally; an elongated subquadrangular cell present below it.

This family is formed to receive the new genus *Polytaxineura*, defined below. It also includes the less well preserved genus *Pholidoptilon* M.D. Zalesky, from the Upper Permian (Kazanian) of Russia, for which its author did not propose a family name, and possibly also the imperfectly preserved genus *Permaeschna* Martynov, also from the Upper Permian of Russia (Iva-Gora). The basal portion of this latter genus is not known and therefore its actual classification must remain uncertain. Should it, however, prove later on to belong to the same family as *Polytaxineura* then the name of the family must be changed to Permaeschnidae Martynov, since Martynov actually defined this family in 1931.

Genus POLYTAXINEURA, n.g.

(Plate xii, figs. 1-3, and Text-figs. 1-3.)

Antenodals of the first and second series for the most part not corresponding, the exceptions being the first, fifth and sixth (cf. recent Aeschnidae). Costal and subcostal spaces narrow, especially towards nodus. Beyond nodus, the costal and radial spaces, as far as they are preserved, are almost entirely devoid of cross-veins, there being only a single postnodal, slightly obliquely placed, at a level just beyond the third cellule below R₂₊₃. Below this, in the radial space, there is a similar cross-vein, followed shortly after, above the fourth descending cross-vein from R₂₊₃, by a second cross-vein placed very obliquely in the opposite direction, i.e., nearly parallel to the subnodus (cf. *Ditaxineura*). In the region of the arculus, about two-fifths of the way from base to nodus, Cu₂ arches strongly upwards in a hump-like fashion and then begins to diverge slightly from the descending free portion of MA above it. There is no posterior arculus, the discoidal cell (*dc*) remaining open basally, and being closed distally by the discoidal vein (*dv*), which descends transversely from MA on to Cu₂ at a point about three-fifths of the way along the elongated subquadrangle (*sq*). Basilar or median space entirely without cross-veins. Cubital space with four oblique cross-veins before the basal side of the subquadrangle; of these, the fourth forms, with the hump of Cu₂ above it, a smaller portion of the hump of 1A below it, and the basal side of *sq*, a small trapezoidal cell which I propose to designate as the *prequadrangle* (*pq*).

About half-way between arculus and nodus, MA gives off a posterior branch, the median supplement, Mspl, concave and separated from MA itself by a single series of cellules. (This must not be confused with the true, original posterior median, MP, which is known to have been suppressed entirely in Lower Permian ancestral forms, and which, in any case, arose quite close to the base of the wing.) 1A also gives off, just distad from the prequadrangle, a similar posterior branch, the anal supplement, Aspl, also slightly concave. The spaces between Mspl,

basal portion of 1A, Aspl and the posterior border are all filled with a polygonal network of cellules for the most part fairly regularly arranged; this formation has suggested the name of the genus.

Nodus complete, the upper fork (end of Sc) being very oblique and about four times as long as the lower fork or nodal cross-vein (*nc*). Subnodus (*Sn*) is continuous with the nodal cross-vein above it and also with R_{4+5} below it; this vein runs parallel to and close above MA.

Where the vein 1A terminates, the posterior margin has a slight bend; probably the same is true where MA terminates, though this portion is not preserved. The pterostigmatic region and apex of the wing are not preserved, but there are some signs of the immediate presence of the pterostigma itself just beyond the break at the end of R_1 . Also a comparison of this region of the wing with that of *Ditaxineura* indicates that the backwardly oblique cross-vein, *k*, should be about in the same relationship to the pterostigma itself as in that genus.

The above definition applies chiefly to the forewing, which is almost completely preserved except for its apical one-fifth. The fragment of the hindwing preserved shows, fortunately, the arculus region, with Rs and MA diverging slightly more from R_1 than in the forewing. From this we may deduce quite legitimately that the hindwing was somewhat broader than the fore. There being no sign of 1A in the broken space below Cu_2 , it is clear also that the subquadrangle was at least somewhat wider than in the forewing, possibly considerably so. The discoidal cell must have been very similar to that of the forewing, but apparently with MA and Cu_2 less diverging owing to the greater obliquity of the former; the distal side of this cell is not preserved.

Genotype, *Polytaxineura stanleyi*, n. sp.

Horizon: Upper Permian of Warner's Bay, New South Wales.

POLYTAXINEURA STANLEYI, n. sp.

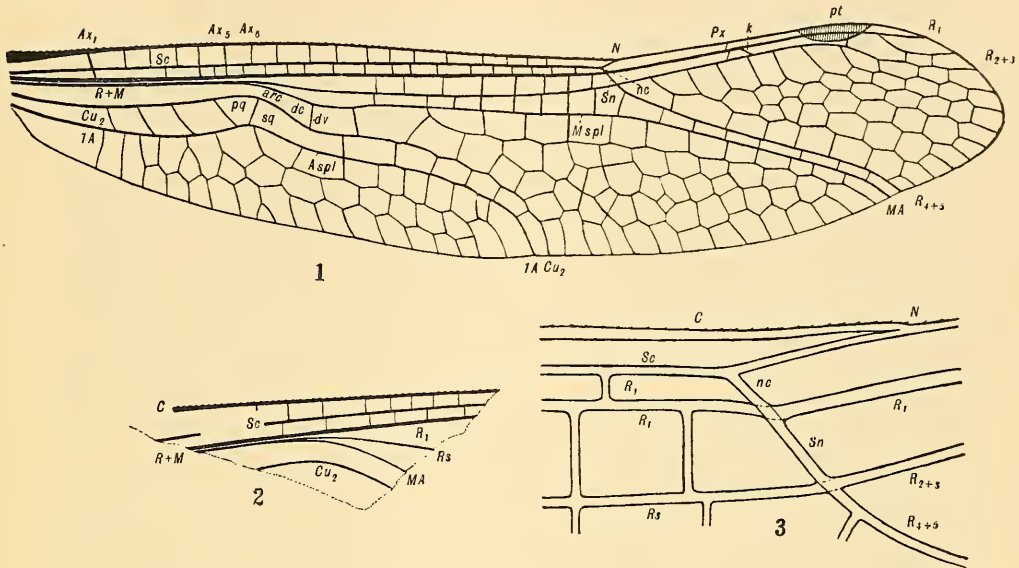
(Plate xii, figs. 1-3; Text-figs. 1-3.)

The preserved portions of this species are as follows:

- A. (1) A nearly complete forewing (Plate xii, fig. 1), obverse impression, with apex to the left; the apical one-fifth missing and also slight breaks on costa just before nodus and on posterior margin about half-way along preserved portion. Rest of the wing very well preserved, except that there is slight damage to the chitinous ridges of Cu_2 and 1A just beyond their humps. The rock is cracked transversely to the wing, and the wing itself very slightly displaced, just distad from these humps; 5 to 6 mm. further distad there is another transverse crack, but without any displacement of the wing. Just distad from nodus there is a third transverse crack, also without displacement of the wing to any extent. The completely restored forewing, with the apex turned to the right, for comparison with other wings, is shown in Text-figure 1.
- (2) (Plate xii, fig. 1). On same piece of rock as above, and lying in its correct position just below the forewing, there is a small portion of the corresponding hindwing (Text-fig. 2), 10 mm. long and triangular in shape, showing C, Sc and R, with the arculus formation and the hump of Cu_2 below it.
- B. (Plate xii, fig. 2.) The counterpart (reverse impression, with apex to right and R_1 concave) of the basal half of the wing mentioned under A (1),

with the humps of Cu_2 and 1A somewhat better preserved than in the obverse impression. A small portion of the hindwing is also preserved, corresponding with A (2).

- C. (Plate xii, fig. 3.) A separate distal piece of the counterpart of A (1), about 12 mm. long, showing the nodus, very well preserved, and the portion of the costal area of the wing basad from it. This piece fits exactly into the distal edge of B.



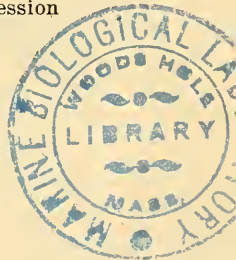
Text-fig. 1.—*Polytaxineura stanleyi*, n.g. et sp. Order Odonata, Suborder Protanisoptera, fam. Polytaxineuridae, n. fam. Restoration of complete forewing, based on the actual specimens as shown in Plate xii. Comstock-Needham Notation except MA, anterior median (convex) of Lameere. *arc*, arculus; *Aspl*, anal supplement; Ax_1 , Ax_5 , Ax_6 , first, fifth and sixth antennodals (corresponding in the first and second series); *dc*, discoidal cell; *dv*, discoidal cross-vein; *k*, oblique radial cross-vein placed after *Px*; *Mspl*, median supplement; *N*, nodus; *nc*, nodal cross-vein; *Pc*, precostal area; *pq*, prequadrangle; *pt*, pterostigma; *Px*, postnodal; *Sn*, subnodus; *sq*, subquadrangle. ($\times 2.6$.) Apex to right.

Text-fig. 2.—*Polytaxineura stanleyi*, n.g. et sp. Fragment of hindwing, with apex placed to right, showing region of arculus. Lettering as in Text-fig. 1. ($\times 4$.)

Text-fig. 3.—*Polytaxineura stanleyi*, n.g. et sp. Forewing, region of nodus. ($\times 11.3$.) Lettering as in Text-fig. 1.

The following description is drawn from all the above specimens:

Forewing.—Length of obverse impression in the actual fossil, 40 mm., representing a complete wing of about 50 mm. in length (Text-fig. 1). Greatest breadth 10 mm. at end of *Aspl*; the breadth only varies between 9 and 10 mm. for most of the length of the wing. The pale grey surface of the rock is mottled irregularly with rust-coloured staining due to oxide of iron. This, however, does not represent any colour-pattern on the wing, as it runs irregularly beyond the wing-impression on to the rock outside.



Precostal area present at base of costa, narrowly wedge-shaped, opaque, coriaceous, its free anterior margin meeting the true costal vein at an angle of about 10° .

Costa (Text-fig. 3, *C*) strongly serrated along its anterior margin. Basally, along the precosta and the first few antenodal cellules, the teeth of the serrations are close together; further distad, they tend to space out and appear as small black denticles wider and wider apart and directed very slightly forwards. Beyond the nodus, they are much fainter, and still more widely spaced.

Antenodals (Text-fig. 1, *Ax*), 17 in the first series (costal) and 20 in the second series (subcostal); only the first, fifth and sixth of the first series corresponding with the second; the costal space is distally free of antenodals for a distance covering the last three of the second series. (Two antenodals of the first series lost in a slight break along the costa in the obverse impression are present in the reverse and are counted in the total.)

Nodus (Text-figs. 1, 3, *N*). At the nodus, *Sc* approaches *C* very gradually, at an angle of about 12° , but the angle which the nodal cross-vein below *Sc* makes with *R* is about 45° . Hence the upper arm of the nodal fork is about four times as long as the lower. The subnodus (*Sn*) continues the slant of the nodal cross-vein (*nc*) above it, and joins *Rs* at its point of bifurcation into R_{2+3} and R_{4+5} , the latter branch continuing the line of *Sn* downwards with a gentle curve towards the apex. The nodus is therefore complete and specialized except for the long approach of *Sc* to the costal margin. As far as can be judged in an incomplete wing, the nodus lies at three-fifths of the total wing-length from the base. This is a primitive character in so far as it indicates a small degree of recession of *Sc* from its ancestral position far along the costal margin.

It should be noted (Text-fig. 3) that both *Sc* and R_1 are somewhat bent at the nodus. The upwardly bent end of *Sc* at the nodus is slightly narrower than the rest of that vein, but the portion of R_1 beyond the nodus is distinctly broader and flatter. The costa itself also becomes narrowed as it approaches its junction with *Sc*, but broadens slightly again immediately afterwards. The marginal serrations become very weak and indistinct distad from the nodus.

Postnodals (Text-fig. 1, *Px*). In the preserved distal portion of the wing, only a single postnodal (*Px*) can be seen between *C* and *R*, with a similar cross-vein just below it. Both of these are situated at a level slightly distad from the third descending vein from R_{2+3} after *Sn*. Slightly distad from the lower of these two cross-veins, and just above the fourth descending vein below R_{2+3} , there is a very oblique, backwardly directed cross-vein (*k*) in the radial space, resembling that found in *Ditaxineura*.

The Pterostigma (Text-fig. 1, *pt*). This is missing in the actual fossil, but its probable structure can be deduced by reference to *Ditaxineura* Till. and *Permaeschna* Mart. (1931a), coupled with the observed fact that *C*, R_1 and R_{2+3} all converge as they approach the pterostigmatic region. In Text-fig. 1, I have restored the pterostigma as elongate but somewhat of the swollen form found in *Ditaxineura* and *Permaeschna*. I have also shown R_{2+3} curving away from R_1 beneath the pterostigma, as it does in these other two genera.

The Arculus (Text-figs. 1, 2, *arc*). From base to beginning of arculus, the two veins R_1 and $Rs+MA$ are quite distinct but contiguous. At the level of the sixth antenodal, $Rs+MA$ begins to diverge very gently from R_1 ; at the level of the seventh antenodal, *MA* separates itself from *Rs* and makes a more markedly downward curve as far as the level of the ninth antenodal, where the discoidal

cross-vein (*dv*) descends from MA on to Cu_2 almost at right angles to the former vein. The arculus is therefore only an *anterior arculus*, the posterior portion (i.e., basal side of discoidal cell) being absent.

The Discoidal Cell (Text-figs. 1, 2, *dc*). This is entirely open basally, but is closed distally by the discoidal cross-vein (*dv*). The discoidal cell in the forewing is widest distally owing to the greater curvature of its posterior side, Cu_2 , compared with its anterior side, MA. In the hindwing (Text-fig. 2), although the discoidal cell is not completely preserved, it can be seen that it must be more rectangular distally owing to the greater obliquity of MA.

Cells in the cubital space. It will be seen (Text-fig. 1) that the basilar or median space is devoid of cross-veins from base right up to the discoidal cross-vein (*dv*). The cubital space, however, possesses four basal cross-veins descending obliquely from Cu_2 to 1A between the base and the humps of these veins. A little distad from the fourth of these veins there is a strong cross-vein arising from the top of the hump of 1A and slanting upwards and outwards to end on Cu_2 just beyond the top of its hump. This cross-vein forms with its two connected main veins and the fourth of the oblique cubital cross-veins already mentioned a trapezoidal figure, the prequadrate (*pq*). Next to this comes the elongated and much curved subquadrate (*sq*), a cell of great importance in the further evolution of this portion of the Odonate wing.

The number of cellules in the part of the forewing preserved is approximately two hundred, indicating that the wing had altogether about two hundred and fifty cellules in it. This is apparently somewhat in advance of the wing of *Pholidoptilon*, and very greatly in advance of the wing of *Ditaxineura*, which had less than sixty.

Type.—*Holotype*, Specimen S 343, A, B and C: A, obverse impression of forewing and small portion of hindwing, with apex to left; B, basal half of reverse impression of same; C, anterior portion of distal half of reverse impression of same.

Locality: Warner's Bay, Lake Macquarie, N.S.W. Found by Mr. Malcolm Stanley, 2nd April, 1935, in a rather large lump of hard pale grey shale having somewhat conchoidal fracture. In the same piece of rock were found part of a leaf of *Glossopteris* and a leaf-scale of same.

AFFINITIES OF THE GENUS POLYTAGINEURA.

The only genus with which the new fossil shows any close affinity is *Pholidoptilon* Zalessky (1932) from the Upper Permian (Kazanian) of Russia. *Pholidoptilon* differs from *Polytagineura* in having much fewer antenodals, those of the first series numbering only thirteen, while those of the second (possibly incomplete) are shown as only seven in Zalessky's figure (l.c., p. 717). The precostal coriaceous area is present in *Pholidoptilon*, but is strongly humped. The first antenodal, complete as in *Polytagineura*, is more oblique, suggesting the brace-vein of recent Plectoptera. *Pholidoptilon* agrees with *Ditaxineura* in possessing no postnodals at all and with *Polytagineura* in having the costal and radial spaces very narrow. The nodus resembles that of *Polytagineura*, but with the upper arm of the nodal fork much shorter. The pterostigma is preserved as a very narrow, elongated, chitinized cell only about two cellules' distance from the nodus. As in *Polytagineura*, R_{4+5} arises from below *Sn*.

Pholidoptilon has the basilar space and arculus very much as in *Polytagineura*, but the humps of Cu_2 and 1A are less marked, and Cu_2 runs parallel with MA as far as the discoidal cross-vein, so that the discoidal cell is an elongated rectangle with the basal side open. The cubital space has a single cross-vein,

slightly oblique, followed by a much more oblique one forming a triangle in the place of the prequadrangle of *Polytaxineura*. Zalesky has jumped to the conclusion that this triangle is homologous with the triangle of Anisoptera, and has explained the line of evolution of this cell from *Pholidoptilon* to Anisoptera along one developmental series, and to Zygoptera along another. The result is that he makes the supratriangle of Anisoptera homologous with the quadrilateral or discoidal cell of Zygoptera, moving the *Pholidoptilon*-triangle (i.e., the prequadrangle of *Polytaxineura*) gradually forward until it comes beneath the discoidal cell.

No student of Odonata could possibly accept this explanation, which controverts the basic work of Needham (1903) on this important phase of venational evolution in Odonata.

We have only to turn to the hindwing of such a genus as *Liassophlebia* Till. (1925, p. 15, fig. 4) to see the falsity of Zalesky's argument. In this wing, the discoidal cell is already practically a pentagon and only requires the development of a longitudinal cross-vein strut to divide it into triangle-plus-supratriangle, exactly along the lines predicted by Needham (1903) in his classical memoir, written long before this genus was discovered. Further, Zalesky has to suppress his triangle entirely in order to bring the Zygoptera into his scheme of evolution. But one could not suppose that a cellule that, on his own argument, was to prove so important in the scheme of evolution of the Anisoptera, would be entirely eliminated in the other recent Suborder.

Zalesky placed *Pholidoptilon* in a new Order, Permodonata, which he claims to be the real ancestor of all recent Odonata. However, when we come to discuss *Ditaxineura* Till., it will readily be seen that the "Order" Permodonata is nothing more than the Suborder Protanisoptera, erected previously (1931) by F. M. Carpenter to contain this latter genus.

Polytaxineura shows distinct affinities (though more distant than with *Pholidoptilon*) with *Ditaxineura* in a number of points of very great importance, viz., the presence of the precostal coriaceous area, the completeness of the oblique first antenodal, the absence or paucity of postnodals, with narrowing of costal and radial spaces beyond the nodus, the origin of R_{2+3} at the subnodus, the very gentle divergence of $Rs+MA$ at the arculus, the form of the discoidal cell, the humped curvature of Cu_2 and $1A$ below the arculus and the presence of a long, curved subquadrangle.

Ditaxineura is more primitive than *Polytaxineura* in the smaller number of antenodals, in the complete absence of postnodals, in the less perfectly formed nodus and subnodus, in the presence of a short basal remnant of Cu_1 and in the very weak formation of the prequadrangle; also, most probably, in the weaker development of the supplement below $1A$. *Ditaxineura* may be somewhat in advance of *Polytaxineura* in the highly specialized form of the pterostigma, and is certainly so in the very regular arrangement of the cross-veins in two gradate series in the distal half of the wing. This latter character, recalling the similar arrangement in the Planipennian family Chrysopidae, is, as far as I know, unique in the Order Odonata.

THE SUBORDER PROTANISOPTERA.

It is now evident that Carpenter's Suborder Protanisoptera must stand, and that it should include the three Permian genera *Ditaxineura* Till., *Polytaxineura*, n.g., and *Pholidoptilon* Zalesky, and possibly *Permaeschna* Martynov also.

The Suborder should be defined as follows:

Odonata with non-petiolate wings, the forewing being slightly longer and narrower than the hind. Precostal coriaceous area present. A true nodus formed at a point beyond half-way along the costa, with a distinct break or bend of the costa at the nodus. Antenodals of both series present; postnodals absent or very few. Arculus formation very weak, no posterior arculus present. Discoidal cell open basally, closed distally by the discoidal vein (*dv*). A long, curved subquadrange present. Cu_2 and 1A both curved upwards in a humped manner below arculus.

Two families can now be defined within the Suborder, as follows:

Family 1. DITAXINEURIDAE.—Basal remnant of Cu_1 present. Nodus and subnodus incompletely formed. Few antenodals present: postnodals entirely absent. Pterostigma much swollen, projecting across radial space almost as far as R_2 . Prequadrangle merely an unspecialized space between two cross-veins. Cross-veins in distal part of wing arranged in two gradate series.

Genus *Ditaxineura* Till. Lower Permian of Kansas.

Family 2. POLYTAXINEURIDAE.—Basal remnant of Cu_1 absent. Nodus and subnodus completely formed and in line. Numerous antenodals present; postnodals absent or very few. Pterostigma probably swollen. Prequadrangle a specialized cell, either trapezoidal or triangular in shape. Cellules and cross-veins much more numerous than in the previous family, but without the specialized arrangement of cross-veins into two gradate series in the distal part of the wing.

Genera, *Polytaxineura*, n.g., *Pholidoptilon* M.D. Zalesky, and possibly also the imperfectly known *Permaeschna* Martynov (1931).

Zalesky did not define a family for his genus *Pholidoptilon*. As the new genus *Polytaxineura* appears to be much better preserved, it seems advisable to name the new family after it rather than after the older but less perfectly known genus. If *Permaeschna* Mart. belongs to this family, the name must be changed to Permaeschnidae Mart.

It will be seen that the Ditaxineuridae foreshadow the Libelluloidea amongst the true Anisoptera, while the Polytaxineuridae foreshadow the Aeschnoidea. It is quite possible that the Ditaxineuridae may prove eventually to be the actual ancestors of the Libelluloidea, giving origin directly to primitive types of Corduliidae, such as *Cordulephya*. But it appears more likely, on present evidence, that the Libelluloidea are a side-branch from the older Aeschnoid complex, and therefore not earlier than Jurassic in geological age. The Polytaxineuridae appear to me to lie in the direct ancestral line of the Anisozygoptera, from which the Aeschnoidea, and therefore most probably the whole of the Anisoptera, were derived in Upper Triassic times, the evolutionary connection being with the Liassogomphidae in the Anisozygoptera and the Petaluridae (more especially Tachopteryginae) in the Aeschnoidea.

Looking backwards geologically, it now appears possible that the Meganeuridae may have been the group with which the Protanisoptera have the closest affinity. Martynov's separation of this family (1932) into a distinct Suborder Meganisoptera would appear to be justified on the single but very important character of the complete absence of a nodus. In other characters the Meganisoptera stand much closer to the Protanisoptera than would appear evident on a cursory inspection; notably in the weak arculus-formation and the humped

curvature of Cu_2 and 1A below the arculus. The more specialized types found in the Protanisoptera have evidently been evolved from a small ancestor with very weak cellule-formation and without any true nodus. Such an ancestor would have to be classified within the Meganisoptera, but not within the Meganeuridae.

The Meganeuridae themselves, though existing in the Upper Carboniferous and Lower Permian, stand far in advance of the true Protodonata (*Protagrion*, *Calvertiella*, *Cockerelliella*, etc.), in which the general scheme of venation is much more complete and more closely approaches that of the Palaeodictyoptera. In the Meganeuridae, as I have previously shown (Tillyard, 1925a), the original main veins MP and Cu_1 are in process of suppression, and only short basal remnants of these veins at the most are still preserved; whereas in the true Protodonata both of these veins remain complete.

I am still unable to satisfy myself that any ancient type lying within the Odonatoid Complex ever possessed more than one true anal vein, viz., 1A. This character is shared with the Order Megasecoptera, as is also another of great importance, viz., the serrated costa. Therefore I must still maintain that we should look for the original ancestor of the whole Odonatoid Complex within the Order Megasecoptera, and not within the Order Palaeodictyoptera, where the anal venation was complete. As the oldest types within the Odonatoid Complex all possess a precostal coriaceous area, we should search for an ancestral form in which this character also appears. Such a form is *Brodica*, which stands at the very base of the Order Megasecoptera, and in which also, as we are fortunate to be able to know, the wing-sheaths of the larva stood upright above the body, thus giving a possible starting-point for the peculiar arrangement in the larvae of Odonata, where the sheath of the hindwing comes to overlie that of the fore.

The discovery of the complete wing of *Ditaxineura* made it necessary, as Carpenter rightly pointed out (1931, p. 136) to abandon my original claim that the Anisozygoptera arose from a Zygoterous or Protozygoterous ancestor, and to accept instead the hypothesis offered by Carpenter that the Anisozygoptera were directly descended from the Protanisoptera. I think that the discovery of the new genus *Polytaxineura* further strengthens this position. We now see that the Protanisoptera stand to recent Anisoptera much as the Marsupials do to Placental Mammals; they are not direct ancestors, but they foreshadow the main types which were destined to be developed, much later, out of the Anisozygoptera. The Ditaxineuridae are definitely "Corduloid" in venational structure, the Polytaxineuridae "Aeschnoid". The true origin of the great Libelluloid Complex still remains to be worked out.

ODONATA INCERTAE SEDIS.

Genus ANTITAXINEURA, n.g. Text-fig. 4.

Wing of fairly large size, with nodus perfectly formed, the upper arm of the nodal fork (Sc) short and quite strongly upturned at an angle of about 30° to costal margin; the lower arm arching strongly downwards to meet R_1 nearly at right-angles and continuing across it as the subnodus (*Sn*) at right-angles to R_1 . A complete series of antenodals present between C and Sc, but none in the subcostal space as far as it is preserved. One postnodal before pterostigma; the latter rather close to nodus, strongly chitinized, with its basal side oblique; in shape it is swollen, apparently much as in *Ditaxineura*, and projects downwards nearly to R_2 , to which it is connected by a cross-vein. Radial space completely free of cross-veins as far as it is preserved, except for this hypostigmatic vein

(*hsv*). At subnodus, R_s appears to bend downwards at a slight angle, but this may be due to fracture of the vein. Just before the level of Sn , R_s is supported by a long strut below it, slanting obliquely downwards and backwards, and there is another similar strut, slightly curved, one cellule's length distad from this; where this second strut drops from R_s two longitudinal veins can be seen, almost lying on top of one another, while a third, much broken, passes obliquely downwards and forwards. The two contiguous longitudinal veins, one of which must certainly be either R_s or R_{2+3} , run together to a point just below the level of the beginning of the pterostigma, where the uppermost of them forks. Assuming the two branches to be R_2 and R_3 , the upper, R_2 , now converges strongly towards the pterostigma as far as the cross-vein *hsv*, where it bends to run parallel to and just below R_1 . The lower branch, R_3 , turns obliquely downwards until it meets a cross-vein, when it also runs parallel to R_2 and very soon gives off a posterior branch.

Genotype, *Antitaxineura anomala*, n. sp.

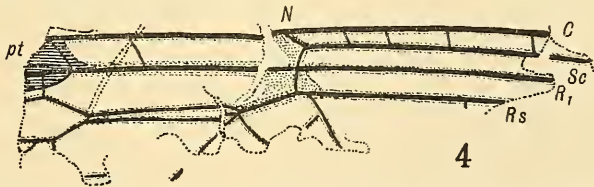
Horizon: Upper Permian of Warner's Bay, New South Wales.

As the above combination of characters should suffice to enable this genus to be recognized when more complete fragments of the wings may happen to be found, I have decided to define it on the very marked characters of the nodal and pterostigmatic regions. The genus is evidently allied to *Ditaxineura* and *Polytaxineura*, but cannot be placed in the same family with either of them. In the highly specialized form of the nodus, it stands well in advance of any Palaeozoic type yet discovered. The pterostigma, as far as it is preserved, is of the Ditaxineurid form, but is preceded by a single postnodal. Evidently the origin of R_{4+5} lies distad from the subnodus, but the fracturing of the main veins in this region forbids us to draw any very definite conclusions as to the course of the branches of R_s . The curious oblique struts below R_s on either side of the subnodus are very peculiar, but it should be noted that the Liassic genus *Liassophlebia* Till. (1925*b*), belonging to the Suborder Anisozygoptera, possesses two similarly directed struts much further apart in the same region. One would not be surprised to find that *Antitaxineura* was a true member of this Suborder.

ANTITAXINEURA ANOMALA, n. sp. Text-fig. 4.

Length of wing-fragment, 14 mm. Length from base of fragment to nodus, approximately 7 mm.; from nodus to distal fracture of pterostigma, also approximately 7 mm.

The specimen represents portion of the obverse impression of a left wing. Four antenodals are clearly preserved, the two most distal ones being closer together than the others. The single postnodal is oblique, as is also the basal side of the pterostigma. All the veins and cross-veins appear to be surrounded



Text-fig. 4.—*Antitaxineura anomala*, n.g. et sp. Order Odonata, *incertae sedis*. Fragment showing portion of anterior part of wing with nodus. Lettering as in Text-fig. 1. Apex to left. ($\times 5.7$.)

with a band of dark pigment; but this is most noticeable along R_1 and R_s beyond the nodus, where the pigment spreads out considerably on either side of the actual vein. The postnodal cross-vein is also strongly pigmented, and the nodal area and pterostigma are widely pigmented, especially the region of the subnodus.

The reverse impression is also preserved, but is only 8 mm. long, most of this belonging to the portion beyond the nodus. The postnodal and pterostigmatic region are better preserved in this than in the obverse, as is also the distal oblique strut below R_s .

Type.—*Holotype*, Specimen P 127, A and B: A, obverse impression; B, reverse impression.

Locality.—Found by Mr. T. H. Pincombe in a piece of hard, medium grey shale from Warner's Bay in 1931.

Possibly belonging to this species is another specimen (P 128) of the basal portion of the posterior margin of a large Odonate wing with the series of cellules just above it. This wing evidently became partly disintegrated and longitudinally folded during the process of fossilization, for most of the main veins can be seen lying upon or slightly across one another. The only clear impression that one can get is of the single series of postcubital cellules of typical Odonate form which evidently intervened between 1A and the posterior margin.

In conclusion, I desire to thank Mr. Walter James, Division of Economic Entomology, C.S.I.R., Canberra, for the excellent photographs shown in Plate xii.

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EXPLANATION OF PLATE XII.

Figs. 1-3.—*Polytaxineura stanleyi*, n.g. et sp. Order Odonata, Suborder Protanisoptera, family Polytaxineuridae, n. fam.

1.—Obverse impression of forewing and small portion of hindwing lying just below it. 2.—Reverse impression of basal portion of same. 3.—Reverse impression of an apical fragment of same, showing nodal region. This fragment fits on to the broken distal portion of fig. 2. (All figures $\times 2\frac{1}{2}$.) (Photos by W. James, Canberra.)

UPPER PERMIAN INSECTS OF NEW SOUTH WALES. V.

THE ORDER PERLARIA OR STONE-FLIES.

By R. J. TILLYARD, M.A., Sc.D., D.Sc., F.R.S., etc.

(Plate xii, figs. 4-5; six Text-figures.)

[Read 30th October, 1935.]

Until recently, the Stone-flies (Order Perlaria) were not known from any geological strata older than the Jurassic. But a more primitive, ancestral Order, the Protoperlaria, was the dominant type of insect in the Lower Permian beds of Kansas and also in beds of the same age in Russia. Therefore it is evident that, somewhere between the Lower Permian and the Jurassic, true Perlaria must have been evolved. In view of the fact that the Australian fauna contains only archaic remnants of this Order, there was a reasonable chance that such forms might be discovered in the Upper Permian beds of New South Wales. This has now proved to be the case. Last year, Mr. T. H. Pincombe made the first discovery, in the form of the greater part of the abdomen of a Perlarian larva, with the two long cerci attached. More recently, in going through some material found by Rev. A. J. Barrett in 1931, I came across portion of a rather large wing which I had classified provisionally as "Neuropteroid". It was possible to uncover this specimen further, with the result that the two series of cross-veins, the medio-cubitals and intercubitals, characteristic of the Order Perlaria, were disclosed in their entirety, and the wing was seen to be definitely that of a true Perlarian.

It is interesting to note that the larval remains, though incomplete, can be definitely correlated with the fossil wing, and most probably belong to the same species. This conclusion is made possible because both the wing and the larval abdomen come very close to an existing Australian genus, *Stenoperla*, belonging to the archaic family Eustheniidae. Yet, in view of the wide differences between the Protoperlaria of the Lower Permian and the descendant Order Perlaria, he would have been a bold man who would have dared to prophesy that the family Eustheniidae extended back as early as the Upper Permian.

The Australian stone-fly fauna consists of only four families, of which three are definitely ancient types, while the fourth consists of a generalized remnant of a more specialized family, the Nemouridae. The three archaic families are the Austroperlidae, confined to Eastern Australia, Tasmania and New Zealand, the Eustheniidae, found in these same regions together with Southern Chile and Patagonia, and the Leptoperlidae, with a similar distribution, but extending more widely in South America and also reaching to Western Australia. A study of their distribution indicates with reasonable certainty that all three families arose in or near Australia, or, more correctly, Euronotia, inclusive of Antarctica, to which it was joined in Permian times. They are all cold-climate groups, but can be graded in a descending series, the larvae of Austroperlidae occurring only in very cold waters, those of the Eustheniidae favouring from very cold to cold waters, and thus extending as far as some mountain streams in Queensland, while those of the Leptoperlidae have a wider range of tolerance, and can stand streams from very cold to only moderate coldness; these also require, for certain species,

less movement of the water than the others. Comparative morphology indicates that the Austroperlidae (Text-fig. 3) are the oldest group of the three. This is best seen in the larvae, in which no special external gills are developed. But the cerci are greatly shortened, and the adult stone-fly has, besides, certain specializations in the wing-venation, notably the perpendicular series of costal veinlets in the forewing, and the thickening of the second interanal cross-vein in the same wing.

The Eustheniidae (Text-figs. 2, 6) are a very ancient group, but have a specialized, predatory larva, extremely active, and provided with five or six paired, filiform gills at the sides of the first five or six abdominal segments respectively. The cerci are not reduced. The general venational scheme is greatly enriched by extra branches of the main veins and by numerous cross-veins. The most striking specialization is the closure of the re-entrant angle between the anal fan and the rest of the hindwing, so that this exceptionally broad wing forms a single wide curve or sweep from apex to base posteriorly. It is not possible to derive the Eustheniidae from the Austroperlidae, but only from some older ancestor resembling them generally, but without the shortened cerci or the venational specializations mentioned.

The Leptoperlidae (Text-fig. 4) are, on the whole, smaller forms, but some genera are of large size and approach the Eustheniidae in appearance. They have sluggish larvae furnished with a rosette of gills around the anus. The adults have the cerci unshortened and the venational scheme very generalized, except for the narrowing of the basal portion of the forewing. Costal veinlets are generally not developed, and there is some fusion of the anal veins in the forewing.

In the present paper, the new fossil form will be compared with selected archaic genera from all three families, and the fossil larva will be shown to agree very closely with that of the genus *Stenoperla*. As the fossil wing also comes very close to that genus, I have no hesitation in classifying the new forms in the existing family Eustheniidae.

It may here be noted that we have now recorded ancient forms of both Odonata and Perlaria from the Upper Permian beds of New South Wales. In view of the fact that the Australian Mayfly fauna contains a complex of genera as ancient as any in the world, one may hazard the prophecy that it should not be long before the third archaic aquatic Order of Insects, the Mayflies, will be found to have existed also in these beds, and I would be inclined to think that whatever Upper Permian genus may be found will almost certainly be closely related to *Tasmanophlebia*, of the archaic family Siphonuridae.

In describing this fossil wing, the notation CuA and CuP will be used for the anterior (convex) cubitus and the posterior (concave) cubitus respectively. The anterior (convex) media will be termed MA; the posterior (concave) media, MP, is absent in all Perlaria, but appears in the Protoperlaria as a partially atrophied vein.

Family EUSTHENIIDAE.

Genus STENOPERLIDIUM, n.g. Pl. xii, figs. 4, 5; Text-figs. 1, 5.

Closely allied to the existing genus *Stenoperla* McL.

Forewing very narrow, being about four times as long as wide, but not particularly narrowed basally. Sc rather short, ending a little beyond half-way in a short fork connecting with both C and R₁. Costal veinlets only moderately

well developed. Radius strongly built, close to Sc, very slightly curved, branched distally in the pterostigmatic area, which is well developed. Rs arising at about one-fourth, leaving R at a very gentle angle, and having a descending series of four pectinate branches distally. MA two-branched, forking just before half-way, the anterior branch curving somewhat upwards towards Rs and then diverging from it again; the posterior branch continues the line of the main stem almost straight. CuA a strong vein, divided into three distally; of these, the first two branches, CuA₁, CuA₂, are anterior and arise by a common stem, while the most posterior branch (CuA₃) continues the line of the main vein directly to the wing-margin. CuP fairly strong, curving concavely to CuA, unbranched. Base of wing, anal area and apex missing; these have been restored by dotted lines in Text-figure 1. In the cross-vein system, the radial cell has only one cross-vein near middle of wing and two or three distally; the radio-median cell is devoid of cross-veins from base to just beyond middle of wing. The distal half of the wing is only moderately supplied with cross-veins, mostly very weakly chitinized. The medio-cubital series is weakly formed, and apparently consists of only three cross-veins. The intercubital series is well formed, consisting of six cross-veins.

Genotype, *Stenoperlidium permianum*, n. sp.

Horizon: Upper Permian of Warner's Bay, N.S.W.

STENOPERLIDIUM PERMIANUM, n. sp. Pl. xii, fig. 4; Text-figs. 1, 5.

Forewing: Length of fragment 22.5 mm., indicating a total length for the complete wing of about 27.7 mm. Breadth 6.3 mm.

The obverse impression lies with its apex to the left; it is preserved from the pterostigmatic region (extreme apex missing) back to within a fifth or less of the base. The preserved part includes all the main venational structures except the primary fork of Cu (which is just missing) and the whole of the anal area and veins. The costal and pterostigmatic veinlets are strongly chitinized; the basal portions of Sc and MA, the extreme base of Rs, its distal portion and branches, and the whole of R₁ are strongly formed, and so is the main stem of CuA. Cross-veins in the spaces between Rs and CuA are mostly weakly formed, except the medio-cubital series, which is fairly strong; in this particular fossil, there are two forked cross-veins, viz., rm (partly displaced by a local break in the rock) and the third medio-cubital, mcu₃; the former is Y-shaped and the latter in the form of an inverted Y; these, however, are to be regarded as only individual peculiarities and not as specific.

There is a definite colour-pattern visible on the fossil wing, consisting of alternating, irregular areas of light and dark pigmentation, together with shading along the main veins, suggestive of the colour-scheme in many recent forms, e.g., some of the New Zealand Leptoperlidae. Deep pigmentation occurs around the end of Sc and the interradiial cross-vein ir, just below it; along R₁, especially distally, and around the pterostigmatic veinlets, spreading out triangularly; also around the distal branches of Rs, less noticeably, and a large, somewhat squarish patch between CuA₁ and CuA₂. The basal portions of Sc and R are also strongly pigmented, and an area of medium shading occurs across the wing in the region of the first and second medio-cubitals, extending right down to CuP. A similar but larger area of medium shading passes in an indistinct band right across the middle of the wing and encloses the two darker areas around ir and between CuA₁ and CuA₂.

Type.—*Holotype forewing*, obverse, Specimen No. B.77a, and reverse, Specimen B.77b (the latter very incomplete, showing only about one-half of Sc and R₁, with the basal portion of Rs and MA).

Discovered by Rev. A. J. Barrett at Warner's Bay in 1931.

Larva of *STENOPERLIDIUM* sp. Text-fig. 5.

Specimen A.73, discovered by Mr. T. H. Pincombe in December, 1933, at Warner's Bay, shows the last seven segments of the abdomen of a Eustheniid larva, together with the two cerci almost complete. Total length of preserved part of abdomen 3.8 mm., of cerci 4.0 mm., representing a length for the complete specimen of about 13 mm., including cerci. Breadth of abdomen at fifth segment, 2.0 mm.

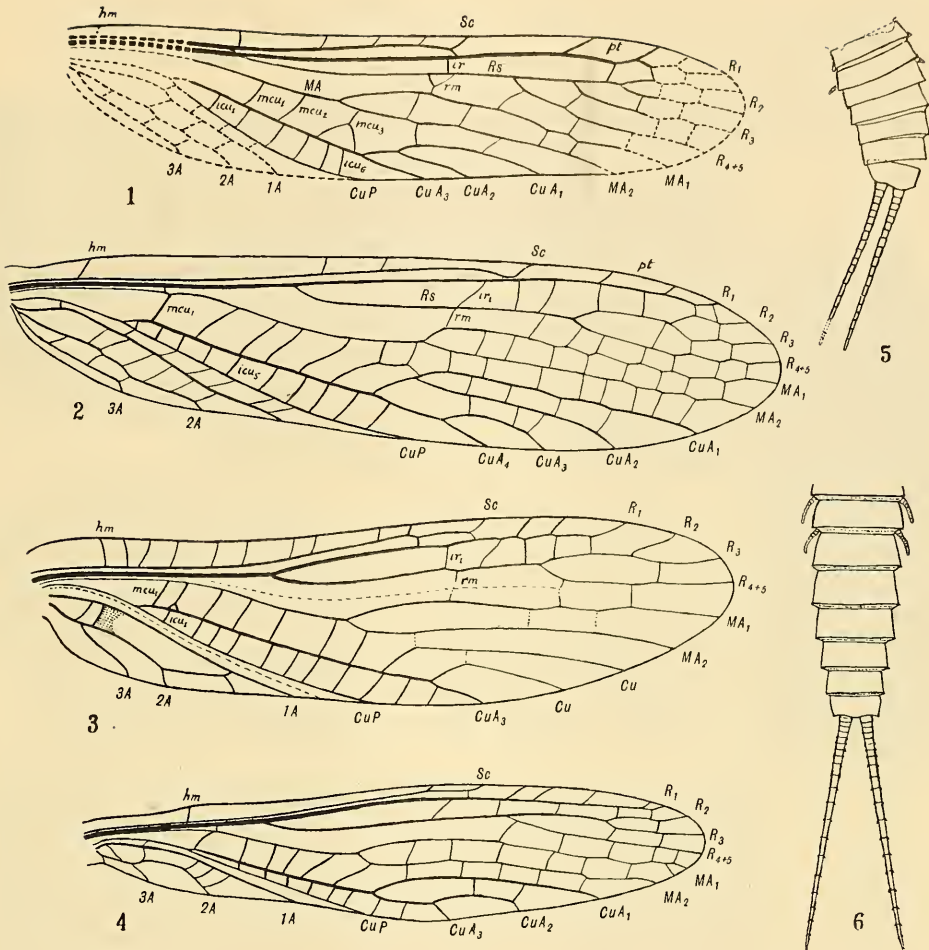
The abdomen is rather broad and somewhat flattened, as is usual in Eustheniid larvae. The most anterior segment visible is the fourth, which is incomplete along its anterior border. The fifth and sixth segments are about equally wide, and thereafter the abdomen tapers posteriorly to the tenth segment. All the segments except the tenth have the postero-lateral margins angulated. The specimen appears to be resting not quite horizontally on the rock and is curved towards the left; on the left side, it is possible to distinguish a finely denticulate lateral margin on segments 4 to 9. The last five segments are evidently without gills; but definite signs of the presence of paired lateral gills on segment 5 are to be seen, that on the right being a short, stumpy process with distinct moniliform annulations, that on the left apparently a small portion of a similar gill, broken off. On the fourth segment, the slight prolongation of the postero-lateral margins also suggests the presence of gills, but all except their basal parts are either broken off or turned in under the abdomen.

The cerci are about as long as the preserved portion of the abdomen; they are separated at bases by a space about equal to their width. The right cercus appears to be complete as to length, but is broken away in two places along its edges; the left cercus is quite complete except for a short portion missing apically. Nineteen segments can be counted on the right cercus, but the segmentation is very indistinct basally. Each cercus is widest basally and tapers gradually to its apex; the basal segments are the shortest, and the segments lengthen gradually to the apex. Some of the divisions are more marked than others (see Plate xii, fig. 5), suggesting that there were rings of pigmentation at these points.

Type.—*Holotype*, Specimen No. A.73. Dated "10.12.33" by T. H. Pincombe, on back.

This larval abdomen may with fair certainty be referred to the genus *Stenoperlidium*, since it differs little from the abdomen of a larva of the existing genus *Stenoperla* McL. If it belongs to the species *S. permianum*, n. sp., as is reasonably probable, then it cannot be a fully grown larva, since its size is too small. In the absence of the thorax and wing-sheaths, this point cannot be determined.

In order that the close resemblance between the larvae of *Stenoperlidium* and *Stenoperla* may be noted, a preparation in 10% KOH was made of the last seven abdominal segments and cerci of a larva of *Stenoperla prasina* (Newm.) from New Zealand (Text-fig. 6). Allowing for the extension of the segments after maceration, so that the soft sutural areas are fully shown (only partly visible in the fossil), the resemblance is remarkably close. It should also be borne in



Text-fig. 1.—*Stenoperlidium permianum*, n.g. et sp. Order Perlaria, Family Eustheniidae. Upper Permian of Warner's Bay, N.S.W. Forewing, restored and with apex to right. The parts missing in the actual fossil (Plate xii, fig. 4) are indicated by dotted lines. Colour-pattern omitted. Total length, about 27.7 mm.

Text-fig. 2.—*Stenoperla prasina* (Newm.). Family Eustheniidae. Forewing. Length 24 mm. Recent, New Zealand.

Text-fig. 3.—*Austroperla cyrene* (Newm.). Family Austroperlidae. Forewing. Length 12 mm. Recent, New Zealand.

Text-fig. 4.—*Trinotoperla australis* Till. Family Leptoperlidae. Forewing. Length 16 mm. Recent, Eastern Australia.

Text-fig. 5.—*Stenoperlidium* sp. Order Perlaria, Family Eustheniidae. Abdomen and cerci of larva. Actual length, including cerci, 7.8 mm.

Text-fig. 6.—*Stenoperla prasina* (Newm.). Family Eustheniidae. Last seven segments of abdomen, with cerci. 10% KOH preparation. Recent, New Zealand. Actual length, including cerci, 23 mm.

mind that it is only in the subfamily Stenoperlinae of the family Eustheniidae (including only two genera, *Stenoperla* McL. from Australia and New Zealand, and *Diamphipnoa* Gerst. from South America) that the larva possesses five pairs of gills on the first five segments, respectively, of the abdomen. In all other genera of this family there are six pairs of gills, on the first six segments of the abdomen respectively.

Affinities of the Fossils.

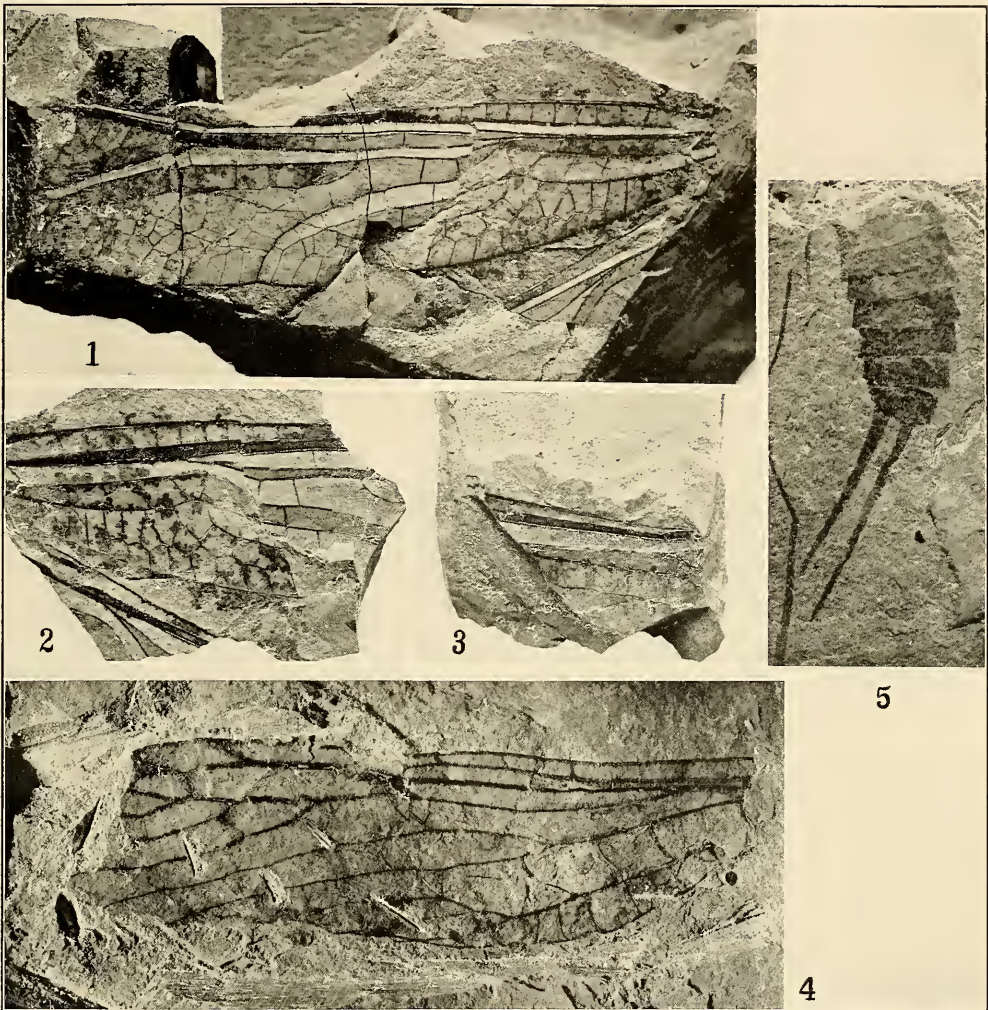
While it seems quite clear that both the forewing and the larval abdomen above described may be placed as directly ancestral to the existing genus *Stenoperla*, and therefore to the family Eustheniidae as a whole (since the genus *Stenoperla* is admittedly the most archaic existing type within the family), it appears advisable to compare the new fossil wing with an archaic type within each of the three families Eustheniidae, Austroperlidae and Leptoperlidae. I have therefore figured the forewing venations of *Stenoperla prasina* (Newm.) (Text-fig. 2), *Austroperla cyrene* (Newm.) (Text-fig. 3), and *Trinotoperla australis* Till. (Text-fig. 4) for comparison.

The principal differences between *Stenoperlidium*, n.g., and *Stenoperla* McL. would appear to be in the shape of the wing, which is broadest before half-way in the fossil genus, but definitely after half-way in *Stenoperla*, and in the greater development of the cross-vein system in the recent genus. We should note, in particular, the closer and more regular arrangement of the distal cross-veins in *Stenoperla*, and the much larger number of cross-veins in both medio-cubital and intercubital series.

Some specimens of *S. prasina* have a more complete series of costal veinlets than that shown in Text-figure 2, thus approaching quite close to *Stenoperlidium* in this respect. The ending of Sc by a sharp bend towards R_1 and then a sudden upward curve to C is a specific character of *S. prasina* only. In the Australian species *S. australis* Till., Sc ends as in the fossil. But this species is usually very heavily veined and does not, in some ways, afford as good a comparison with the fossil as does *S. prasina*. *S. australis* agrees with the fossil more closely than *S. prasina* in the mode of origin of Rs, which is less abrupt and also somewhat nearer the base than in *S. prasina*. Both species of *Stenoperla* differ from the fossil in having Sc and R closer together and less strongly formed, and also in having the pterostigmatic area narrower than in the fossil. In *S. australis*, there are usually cross-veins developed in the radio-median space before the primary fork of MA, while CuP is straighter, nearer to CuA and lies more definitely in a straight furrow. Both species of *Stenoperla* agree with the fossil in the upward arching of the anterior branch of MA and in the continuity of the posterior branch with the main stem. They also agree in the type of branching of CuA, though there are usually four branches instead of three, the extra one being formed by forking of CuA₃. This, however, is not a constant character. As the humeral veinlet is present in all Eustheniidae, it has been restored in the fossil in Text-figure 1.

It comes as a great surprise, in view of our knowledge of the Lower Permian Order Protoperlaria, that this Upper Permian fossil should stand so definitely within the family Eustheniidae and so extremely close to the existing genus *Stenoperla*.

There is no other Order known in which the resemblance between Upper Permian and recent forms is so close, except, indeed, it be so in the Cockroaches,



1-3.—*Polytaxineura stanleyi*, n.g. et sp. 4.—*Stenoperlidium permianum*, n.g. et sp.
5.—*Stenoperlidium* sp.